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Effects of exercise modality on patterns of ventilation and respiratory timing

David M. Caretti, Patricia C. Szlyk and Ingrid V. Sils

Comparative Physiology Division, U.S. Army Research Institute of Environmental Medicine, Natick, MA, USA

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Abstract. Ventilatory patterns and respiratory timing were measured in 14 subjects during cycling (CYC) and treadmill exercise (TM) at similar leg frequencies (fLEG) to determine if mode of exercise affects patterns of ventilation and respiratory timing. Measurements of breathing frequency (fR), tidal volume (VT), expired ventilation ($\dot{V}$E), and inspiratory (TI) and expiratory (TE) time were obtained at fLEG of 50, 70, and 90 rev·min^{-1} (rpm) for CYC and at similar incremental fLEG (strides·min^{-1}; spm) during TM achieved by increasing belt speed at 0% grade. CYC exercise intensity was ~50% $\dot{V}_{O_2max}$ at all fLEG, whereas $\dot{V}_{O_2}$ increased progressively with TM. fR increased significantly ($P < 0.001$) with increasing fLEG of TM (20.5 ± 4.6, 25.4 ± 5.8, and 36.3 ± 7.6 breaths·min^{-1}; $\bar{x}$ ± SD), but during CYC fR changed significantly ($P < 0.05$) only between fLEG of 70 and 90 rpm (25.0 ± 5.9 *vs* 28.5 ± 6.9 breaths·min^{-1}). Both average breath TI and TE obtained by grouping into incremental ranges of fR decreased significantly ($P < 0.05$) with increasing fR up to 36 breaths·min^{-1} and the relationships of TI and TE to fR, TI to TE, and central inspiratory drive (VT/TI) to $\dot{V}$E were the same for CYC and TM. Group average fR and fLEG were synchronized during TM, but individual subjects did not exhibit a high degree of entrainment. This study shows respiratory timing patterns to be independent of mode of exercise over the range of fR observed when describing patterns by grouping into incremental ranges of fR.

Control of breathing, pattern, exercise; Exercise, mode, pattern of breathing; Mammals, humans; Pattern of breathing, exercise modes

Breathing patterns and respiratory timing variables have been investigated during various types of exercise in both animals and humans to determine whether neurogenic influences, originating in the exercising limbs, contribute to exercise hyperpnea. Several investigators have observed synchronization of breathing frequency to leg frequency during rhythmic exercise, suggesting that the ventilatory response to exercise can be accounted for by limb reflexes (Bannister *et al.*, 1954; Hey *et al.*, 1966; Asmussen, 1973; Bechbache and Duffin, 1977; Jasinskas *et al.*, 1980; Bramble, 1983; Bramble and Carrier, 1983). Others have concluded that afferent input from muscle receptors is not a component of exercise ventilation (Sipple and Gilbert, 1966; Kelman and Watson, 1973; Kay *et al.*, 1975a; Clark *et al.*, 1983).

Correspondence to: D.M. Caretti, Commander, U.S. Army CRDEC, Attn: SMCCR-PPI/David M. Caretti, Aberdeen Proving Ground, MD 21010-5423, USA.

Measurements of tidal volume and durations of the inspiratory and expiratory phases of the ventilatory cycle correspond to variables that can be used to characterize the neural regulation of respiration. Specifically, the ratios of tidal volume to inspiratory time and of inspiratory time to total breath duration serve as indices of central inspiratory drive and respiratory timing, respectively (Milic-Emili and Grunstein, 1976). Evidence of whether these variables are affected by different modes of exercise is limited (Kay *et al.*, 1975b; Clark *et al.*, 1983). Furthermore, in order to determine if differences in breathing patterns occur between exercise modes, ventilatory patterns should be measured under the same conditions (*i.e.* environment, leg frequency) for each mode. However, these considerations have often been overlooked.

Therefore, the present study was undertaken to determine (1) the effects of three progressively increasing leg frequencies on ventilatory patterns and respiratory timing; and (2) the effects of two modes of exercise, cycle ergometry and treadmill exercise, on these variables.

Methods

Fourteen healthy male subjects (age 28.4 ± 7.1 years; $\bar{x} \pm$ SD) volunteered for this study. The study was approved by the U.S. Army Research Institute of Environmental Medicine in accordance with Army Regulation 70-25 for the use of human volunteers. After informed consent was obtained, subjects completed a health and physical activity questionnaire and measurements of height and body weight were taken. One day before testing each subject performed a maximal oxygen consumption ($\dot{V}_{O_2,max}$) test on a cycle ergometer. Briefly, subjects pedaled continuously at 60 rev·min^{-1} (rpm) while workload was increased 50 Watts every 3 min until exhaustion or until pedal frequency could not be maintained. Following a 5-min rest period, subjects exercised again starting at a workload 50 Watts lower than the highest workload that they had obtained. After 3 min, intensity was increased by 50 Watts and subjects continued to exercise to exhaustion. It was determined that $\dot{V}_{O_2,max}$ had been obtained if oxygen consumption ($\dot{V}_{O_2}$) during this second maximal exercise bout did not exceed peak values from the first exhaustive test. $\dot{V}_{O_2,max}$ values were used for determination of relative oxygen consumption during subsequent testing. Subjects had relatively wide ranges of body weights (57.97–110.52 kg) and physical fitness levels ($\dot{V}_{O_2,max}$: 38.77–61.60 ml·kg^{-1}·min^{-1}).

This investigation involved 4 separate days of testing. Subjects randomly performed one exercise session on a cycle ergometer (Collins Pedalmate) and a treadmill on either of the first 2 testing days. During cycle ergometry, subjects exercised continuously at an estimated intensity of 50% $\dot{V}_{O_2,max}$ at leg frequencies (fLEG) of 50, 70, and 90 rpm for 15 min each. Subjects maintained leg frequencies by watching a speedometer and were individually monitored by technical personnel to assure sustainment of the respective frequency. Also, fLEG were measured in conjunction with sequential breath measurements during the last 5 min of exercise at each frequency interval by counting the number of pedal revolutions for a given amount of time.

During treadmill trials, subjects walked, or jogged, at zero percent grade at three treadmill speeds adjusted to elicit fLEG of 50, 70, and 90 strides$\cdot$min^{-1} (spm), similar to the frequencies of cycling. Leg frequencies were measured as during cycling but by counting the number of strides for a given amount of time. For both modes of exercise subjects were unaware that these measurements were being taken. Each fLEG involved 15 min of total exercise. Six days later subjects repeated both the cycling and treadmill regimens on 2 separate days. Speeds selected on each subject's initial treadmill exercise session were duplicated for the final bout of treadmill exercise.

Heart rate (HR), fLEG, breathing patterns, and expired gases were monitored using the same procedures for both cycling and treadmill trials. Heart rate was monitored continuously from 3-channel ECG leads using a Hewlett-Packard telemetry system. A semi-automated system consisting of a Hewlett-Packard 85B computer and digital voltmeter interfaced with a gas meter (Parkinson-Cowan), oxygen analyzer (Applied Electrochemistry S3A), and carbon dioxide analyzer (Beckman LB2) was used to collect and analyze expired gases from the expiratory side of a Collins J-valve. Expired gases were collected on-line during the last 5 min of exercise at each fLEG. Sustained levels of $\dot{V}_{O_2}$ for 4–5 min signified that a steady-state of exercise had been obtained.

Patterns of ventilation and respiratory timing were measured concurrently with expired gases. A pneumotachometer (Hans Rudolph), connected to a pressure transducer (Validyne MP45), carrier demodulator (Validyne CD15), and a polygraph (Western Graphtech), was affixed to the inspiratory side of a Collins J-valve to measure inspiratory air flow. After subjects inserted the mouthpiece connected to the Collins J-valve into their mouth, a noseclip was put in place and recordings of ventilatory flow were monitored on the polygraph. Once the subject felt comfortable with the mouthpiece and breathing apparatus, based on steady polygraph readings and visual observation, measurements of expired gases and breathing patterns began. Measurements of breathing frequency (fR), tidal volume (VT), expired ventilation ($\dot{V}$E), and inspiratory (TI) and expiratory (TE) time were obtained on 3 separate occasions during the last 5 min of each fLEG interval. Measurements were averaged for each incremental leg frequency. Average ratios of pedaling or stepping frequencies to breathing frequency were calculated to test for synchronization of breathing frequency to leg frequency.

Breath-by-breath analyses of respiratory timing were taken from the 3 data collection periods during the last 5 min of exercise for each fLEG. Up to ten sequential breaths (maximum of 30 breaths from each steady-state) were analyzed for TI, TE, and total breath duration (TTOT). Instantaneous breath frequency (fR) (60/TTOT) and respiratory timing (TI and TE) were calculated. For analysis, individual breath data for each mode of exercise were grouped into incremental ranges of breath frequency (3 breaths$\cdot$min^{-1} intervals).

With a Complete Statistical System (CSS) software package (StatSoft 1987), data were analyzed within and between exercise modes using ANOVA and Scheffe's *post-hoc* analyses. The null hypothesis was rejected at the $P<0.05$ level. All values represent mean $\pm$ SD.

Results

No differences existed between each cycling and each treadmill trial. Therefore, data from both cycling trials were pooled and analyzed as one data set *vs* the pooled treadmill data.

Exercise intensity

Expressed as percent $\dot{V}_{O_2,max}$, the average intensity of exercise during cycling was not significantly different at the three different pedal frequencies (Table 1). For treadmill exercise, subjects utilized a significantly ($P<0.001$) greater percentage of $\dot{V}_{O_2,max}$ with each increase in stride frequency. The $\dot{V}_{O_2}$ during cycling was significantly ($P<0.05$) different from treadmill exercise at all leg frequencies. Heart rate responses differed significantly ($P<0.001$) between modes at the lowest and highest fLEG, and increased significantly ($P<0.001$) with progressively increasing fLEG during treadmill exercise (Table 1).

Ventilatory and respiratory timing patterns

Average values of fR, VT, $\dot{V}$E, and TI and TE at each fLEG are presented in Table 2. No significant changes in VT or $\dot{V}$E occurred with increasing fLEG during cycling. Treadmill exercise elicited a significant ($P<0.001$) increase in VT when stride frequency increased from 70 to 90 spm, and $\dot{V}$E increased significantly ($P<0.005$) with each fLEG increase.

For both modes, as fLEG increased, fR increased progressively. With incremental fLEG, elevations in fR during cycling were less than the corresponding increases during treadmill exercise. Increases in fR at each incremental fLEG were significant ($P<0.001$) during treadmill exercise, but during cycling increases in fR were significant ($P<0.05$) only when subjects progressed from 70 to 90 rpm. At the highest fLEG, fR was significantly ($P<0.001$) greater for treadmill *vs* cycling exercise. As fR increased with

TABLE 1

Average exercise intensity and heart rate responses

Measure	Cycling (rpm)			Treadmill (spm)		
	50	70	90	50	70	90
$\%\dot{V}_{O_2,max}$	46.4	47.1	53.3	20.7[a]	35.8[a,b]	68.0[a,b]
	(10.6)	(13.1)	(14.5)	(7.2)	(12.8)	(11.7)
HR	114.7	118.4	123.1	86.8[a]	112.6[b]	156.7[a,b]
	(17.0)	(17.6)	(22.5)	(11.7)	(26.7)	(18.0)

Values are means ($\pm$ SD) of measures taken at each leg frequency interval ($n=28$). $\%\dot{V}_{O_2,max}$ = percent of maximal oxygen consumption; HR = heart rate (beats·min^{-1}).

[a] Significant difference between modes of exercise.

[b] Significant difference between sequential leg frequency intervals.

TABLE 2

Average ventilatory and respiratory timing patterns

Measure	Cycling (rpm)			Treadmill (spm)		
	50	70	90	50	70	90
VT	1.67	1.64	1.72	0.95[a]	1.18[a]	1.83[b]
	(0.49)	(0.41)	(0.39)	(0.35)	(0.41)	(0.46)
$\dot{V}$E	37.9	39.5	44.6	18.4[a]	28.7[a,b]	63.7[a,b]
	(7.9)	(7.6)	(9.5)	(5.3)	(9.6)	(16.8)
*f*R	23.2	25.0	28.5[b]	20.5	25.4[b]	36.3[a,b]
	(5.6)	(5.9)	(6.9)	(4.6)	(5.8)	(7.6)
TI	1.17	1.11	1.07	1.25	1.07[b]	0.82[a,b]
	(0.36)	(0.32)	(0.40)	(0.47)	(0.32)	(0.21)
TE	1.57	1.44	1.33	1.99[a]	1.50[b]	0.95[a,b]
	(0.48)	(0.34)	(0.37)	(0.52)	(0.40)	(0.32)

Values are means ($\pm$ SD) of measures taken at each leg frequency interval ($n = 28$). VT = tidal volume (L); $\dot{V}$E = expired ventilation ($L \cdot min^{-1}$); *f*R = breathing frequency ($breaths \cdot min^{-1}$); TI = inspiratory time (sec); TE = expiratory time (sec).

[a] Significant difference between modes of exercise.

[b] Significant difference between sequential leg frequency intervals.

progressively increasing leg frequencies during treadmill exercise, both average breath TI and TE decreased significantly ($P < 0.05$). Average breath TI and TE decreased with increasing *f*LEG during cycling, but changes were not significant. In addition, average breath TE was greater than TI at all three leg frequencies. This relationship was not different between modes of exercise.

Average group values of the breath-by-breath relationship of TI and TE to *f*R obtained by binning into incremental ranges for both modes of exercise can be seen in Fig. 1. For the 14 subjects a total of 3744 breaths, 1538 during cycling and 2206 during treadmill exercise, were measured. The relationships of TI and TE to *f*R were similar between modes of exercise. Average TI and TE decreased significantly ($P < 0.05$) with increasing *f*R up to approximately 36 $breaths \cdot min^{-1}$ and the absolute change in TE was greater than that for TI. At *f*R greater than 36 $breaths \cdot min^{-1}$ average TI did not change significantly, whereas TE continued to decrease significantly. Only between *f*R of 36–39 $breaths \cdot min^{-1}$ during cycling was the change in TE not significant. Average duration of TI was significantly ($P < 0.05$) less than TE at all *f*R below 39 $breaths \cdot min^{-1}$.

The relationships of TI and TE to *f*R were quantitatively similar between cycling and treadmill modes of exercise at *f*R above 12 $breaths \cdot min^{-1}$. However, at the single *f*R bin below 12 $breaths \cdot min^{-1}$ average TE during treadmill exercise was significantly greater compared to cycling.

Average durations of TE *vs* TI obtained from the same binned incremental *f*R are plotted in Fig. 2 against isolines of the proportion of total breath duration spent in inspiration (TI/TTOT) for both modes of exercise. As breath TI and TE decreased with

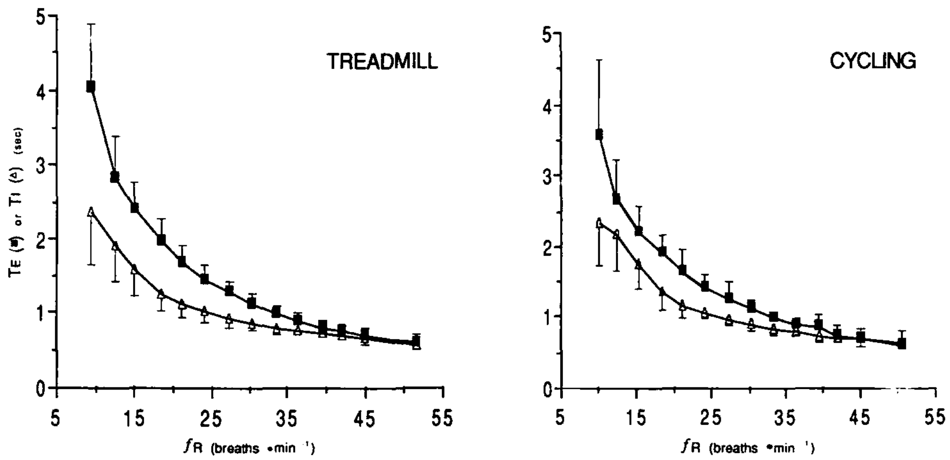

Fig. 1. Relationship of average TI (△) and TE (■) binned by sequential ranges of *f*R for both modes of exercise. Data represent mean ± SD for the subject group. Number of breaths analyzed for treadmill exercise was 2206 (n = 15, 50, 104, 150, 193, 242, 234, 221, 166, 130, 251, 204, 138, and 108 for bins 1–14, respectively). 1538 breaths were analyzed for cycling (n = 12, 27, 110, 110, 231, 276, 271, 185, 134, 89, 37, 33, 19, and 4 for bins 1–14).

increasing *f*R, TI/TTOT was reduced and the ratio approached 0.50. This relationship was the same for both modes of exercise.

Respiratory drive

Central inspiratory drive (VT/TI), an index of inspiratory motor input, was plotted against V̇E in Fig. 3 for both modes of exercise. During both cycling ($r = 0.97$; $P < 0.001$)

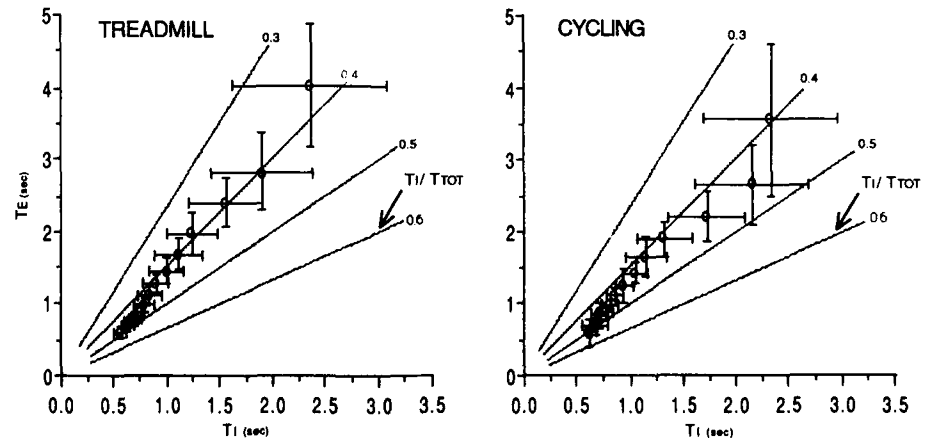

Fig. 2. Average values ± SD of TE versus TI obtained from the same sequential ranges of *f*R for both exercise modes. The proportion of time spent in inspiration during the total breath cycle is represented by the superimposed isolines of TI/TTOT.

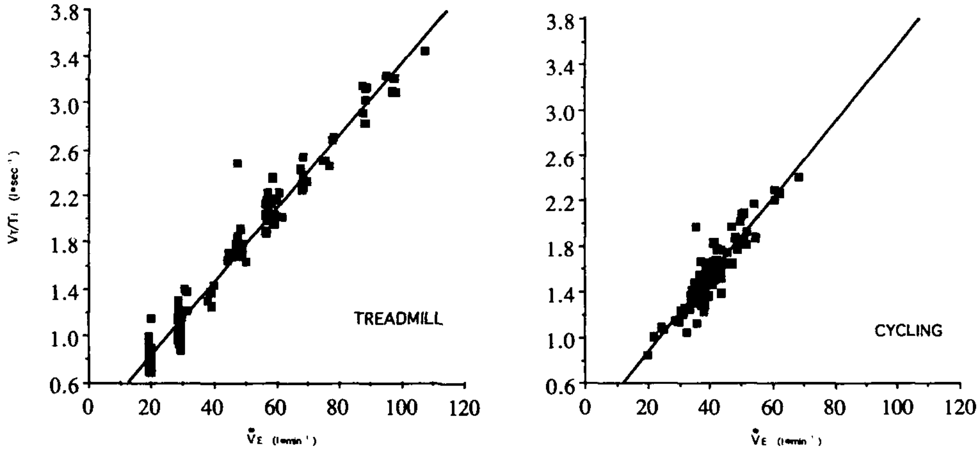

Fig. 3. Central inspiratory drive (VT/TI) plotted against $\dot{V}$E for both modes of exercise. Data represent average values of VT/TI and $\dot{V}$E obtained during each of the 3 leg frequency intervals.

and treadmill exercise ($r = 0.98$; $P < 0.001$) central inspiratory drive was positively correlated to $\dot{V}$E, and no differences were found between exercise modes.

Influence of limb movement on breathing frequency

To evaluate the possibility of synchronization of *f*R to leg frequency (*f*LEG), or entrainment, calculations of the ratio of *f*LEG to *f*R (*f*LEG/*f*R) were made. Ratios of *f*LEG/*f*R were identical for the subject group at each leg frequency (2.6 ± 0.8, 2.7 ± 0.6, and 2.6 ± 0.7) during treadmill exercise. Average group ratios of *f*LEG/*f*R increased significantly ($P < 0.001$) for the group with increasing leg frequencies during cycling (2.3 ± 0.7, 2.9 ± 0.6, and 3.4 ± 0.9).

Discussion

Ventilatory patterns and respiratory timing and drive

Changes in *f*R have generally been attributed to changes in TE rather than TI, in both resting animals and humans (Newsom-Davis and Stagg, 1975; Sullivan *et al.*, 1978). Kay *et al.* (1975b) and Clark *et al.* (1983) also reported this relationship during exercise in man. However, Iscoe *et al.* (1983) and Jennings and Szlyk (1985) reported that both TI and TE change as *f*R spontaneously changes for dogs and cats, respectively, while breathing room air. Rather than using consecutive breaths with varying *f*R to average timing, these latter investigators grouped TI and TE by individual breath *f*R. This unique approach enabled comparisons of TI and TE at a given *f*R in response to a stimulus with timing at the same *f*R under control conditions. By averaging timing from consecutive breaths with variable *f*R, previous investigators masked not only the differences in timing related to *f*R but also the considerable amount of variability found

in breathing patterns (Kay *et al.*, 1975b; Newsom-Davis and Stagg, 1975; Sullivan *et al.*, 1978; Clark *et al.*, 1983). Kay *et al.* (1975b) further restricted interpretation of their data by eliminating any breath if VT was greater than one and a half times the mean or if TI was two times greater than the mean, and by eliminating the two breaths immediately following any mis-recorded breath. Clark *et al.* (1983) averaged timing patterns for each minute of an exercise session rather than for *f*R, thus failing to actually compare timing at a given breath *f*R.

In our data analysis we employed the technique of grouping TI and TE by individual *f*R and found that the relationship of respiratory timing and *f*R during submaximal exercise in man was qualitatively similar to that of resting, awake cats and dogs (Iscoe *et al.*, 1983; Jennings and Szlyk, 1985). As *f*R increased up to approximately 36 breaths·min^{-1}, both TI and TE decreased significantly (Fig. 1). Above this *f*R, average TI was relatively fixed, whereas TE continued to decrease significantly. Average TI was less than TE at *f*R below 39 breaths·min^{-1}, but as *f*R increased above this frequency the durations of TI and TE became equal. This relationship of TI and TE to *f*R was similar for both treadmill exercise and cycling, and for a given *f*R there was a predictable TI and TE.

At a given *f*R above 12 breaths·min^{-1}, the TI and TE for treadmill exercise were indistinguishable from the TI and TE for cycling (Fig. 1). Significantly longer average TE was observed at *f*R less than 12 breaths·min^{-1} during treadmill compared to cycling exercise. This difference resulted from the greater variability of TE measured at the lowest *f*R interval during cycling (3.55 ± 1.06 sec; $n = 12$) compared to treadmill exercise (4.02 ± 0.85 sec; $n = 15$). Sequential breath measurements also showed a large degree of variability in TI and TE below *f*R of 18 breaths·min^{-1}. As breath *f*R increased above 18 breaths·min^{-1}, respiratory timing decreased and varied less at a given *f*R.

It has been reported that during maximal exercise average TE becomes slightly less than TI at an average *f*R of 62 breaths·min^{-1} (Clark *et al.*, 1983). In the present study, with the greater decrease in TE than TI with increasing *f*R, the amount of time spent in inspiration (TI/TTOT) increased from approximately 0.40 to 0.50 for both exercise modes. At the highest recorded *f*R during cycling and treadmill exercise, average durations of TI essentially equalled those of TE. However, during cycling the duration of TI was longer (not significantly) than TE, and a slight 'cross-over' of TE and TI was observed at a *f*R of approximately 45–50 breaths·min^{-1}. Our inability to see a sustained 'cross-over' of TE and TI during exercise probably is due to the lower *f*R of our subjects compared to those reported during maximal exercise. Numerous reports suggest that central hypothalamic mechanisms probably regulate breathing when TI/TTOT exceeds 0.50 (Jennings and Szlyk, 1985; Szlyk and Jennings, 1987).

When respiratory timing data was analyzed by averaging timing from sequential breaths of different frequencies we found that average duration of TE was longer than TI at each of the three leg frequency intervals (Table 2). This was true for both modes of exercise. However, this analysis suggests that changes in TI and TE did not contribute significantly to increasing *f*R during cycling. In contrast, grouping TI and TE by individual *f*R showed that both TI and TE decreased significantly with increasing

f_R during cycling. This analysis supports the concept that averaging timing from sequential breaths obscures the differences of timing related to individual f_R. Furthermore, averaging sequential f_R at each f_{LEG} also obscured measures of individual f_R. Averaging timing from sequential breaths showed that T_I and T_E between exercise modes were significantly shorter during treadmill exercise at the highest leg frequency. The higher f_R exhibited at this leg frequency level during treadmill exercise would account for these observed differences. This greater f_R, in turn, probably resulted from the greater oxygen consumption observed between treadmill *vs* cycling modes at the highest leg frequencies.

Clark *et al.* (1983) reported two linear relationships of T_E to T_I, one during walking and the second while running. One relationship had a shallow slope that included all values of respiratory timing obtained during exercise and T_I/T_{TOT} was approximately 0.50. The second, obtained during walking and when at rest, displayed a steeper slope, and T_E was longer than T_I. We did not observe two distinct linear relationships when comparing breath-by-breath durations of T_E and T_I during either cycling or treadmill exercise at the three different leg frequencies. However, no rest or recovery data were included in our analysis.

As shown in Fig. 3, mean inspiratory flow rate (V_T/T_I) increased linearly as $\dot{V}_E$ increased during cycling and treadmill exercise. Thus, V_T/T_I appeared to be an index of central inspiratory drive as previously reported (Milic-Emili and Grunstein, 1976). Also, Milic-Emili and Grunstein (1976) and Clark *et al.* (1983) have stated that the relationship of V_T/T_I to $\dot{V}_E$ will be linear as long as T_I/T_{TOT} remains constant. In our experiments T_I/T_{TOT} varied from approximately 0.40 to 0.53 during cycling and from 0.38 to 0.53 during treadmill exercise as $\dot{V}_E$ increased. This finding indicates that central inspiratory drive is linearly related to $\dot{V}_E$ independent of respiratory timing or modes of exercise. Similar results have been observed for air and CO_2 inhalation in cats (Jennings and Szlyk, 1985; Szlyk and Jennings, 1987).

The relationships of T_E and T_I (Fig. 2) and V_T/T_I and $\dot{V}_E$ (Fig. 3) were indistinguishable between cycling and treadmill exercise. The drive for ventilation, therefore, was the same for the three leg frequency levels during both modes of exercise. This observation indicates that these relationships are not influenced by exercise mode.

Entrainment

The possibility of entrainment, or synchronization of breathing frequency to exercise rhythm, has long been recognized, but has been difficult to detect (Bannister *et al.*, 1954; Hey *et al.*, 1966; Kay *et al.*, 1975a; Bechbache and Duffin, 1977; Jasinskas *et al.*, 1980; Bramble and Carrier, 1983; Clark *et al.*, 1983). The results of the present study showed average ratios of f_{LEG}/f_R to be constant with progressive increases in leg frequency during treadmill exercise, but not during cycling. However, based on average f_{LEG}/f_R ratios for each individual subject, only 64% of the subjects had constant ratios at all leg frequencies during treadmill exercise.

It has been suggested that exercise intensity may influence entrainment (Bechbache and Duffin, 1977; Jasinskas *et al.*, 1980; McMurray and Ahlborn, 1982). In the present

study, no entrainment was observed when exercise intensity remained unchanged while cycling. During treadmill exercise, intensity increased significantly with increasing fLEG and 64% of the subjects appeared to entrain fR to fLEG. These findings tend to support that metabolic rate may determine the degree of subject entrainment. Also, since timing patterns of ventilation and central inspiratory drive did not differ between exercise modes, the relationship of respiratory timing to fR appeared not to be influenced by entrainment. However, since our subject population did not exhibit a high degree of entrainment, no definite conclusions could be made about the effects of exercise intensity on entrainment, or the influence of entrainment on timing patterns and inspiratory drive.

Thus, the quantitative description of the variability of ventilation on a breath-by-breath basis in this study shows that decreases in the duration of both expiratory and inspiratory time contribute significantly to increases in breathing frequency. Also, the relationship of timing patterns to breathing frequency is independent of mode of exercise, and intensity, over the range of leg and breathing frequencies observed. Qualitatively, our data indicate that the relationship between breath timing and breathing frequency in man is similar to that of cats and dogs. Establishment of this fundamental relationship between species may allow for stronger comparisons between species when evaluating the effects of various stimuli on respiratory timing.

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Disclaimer. The views, opinions, and/or findings contained in this report are those of the authors and should not be construed as official Department of the Army position, policy, or decision, unless so designated by other official documentation. Human subjects participated in this investigation after giving their free and informed voluntary consent. Investigators adhered to AR 70-25 and USAMRDC Regulation 70-25 on Use of Volunteers in Research.

References

Asmussen, E. (1973). Ventilation at transition from rest to exercise. *Acta Physiol. Scand.* 89: 68–78.

Bannister, R.G., D.J.C. Cunningham and C.G.Douglas (1954). The carbon dioxide stimulus to breathing in severe exercise. *J. Physiol.* 125: 90–117.

Bechbache, R.R. and J. Duffin (1977). The entrainment of breathing frequency by exercise rhythm. *J. Physiol.* 272: 553–561.

Bramble, D.M. (1983). Respiratory patterns and control during unrestrained human running. In: Modelling and control of breathing; edited by B.J. Whipp and D.M. Wiberg. Amsterdam: Elsevier, pp. 213–220.

Bramble, D.M. and D.R. Carrier (1983). Running and breathing in mammals. *Science* 219: 251–256.

Clark, J.M., F.C. Hagerman and R. Gelfand (1983). Breathing patterns during submaximal and maximal exercise in elite oarsmen. *J. Appl. Physiol.: Respirat. Environ. Exercise Physiol.* 55: 440–446.

Hey, E.N., B.B. Lloyd, D.J. Cunningham, M.G. Jukes and D.P. Bolton (1966). Effects of various respiratory stimuli on the depth and frequency of breathing in man. *Respir. Physiol.* 1: 193–205.

Iscoe, S., R.B. Young and D.B. Jennings (1983). Control of respiratory pattern in conscious dog: effects of heat and CO_2. *J. Appl. Physiol.: Respirat. Environ. Exercise Physiol.* 54: 623–631.

Jasinskas, C.L., B.A. Wilson and J. Hoare (1980). Entrainment of breathing rate to movement frequency during work at two intensities. *J. Respir. Physiol.* 42: 199–209.

Jennings, D.B. and P.C. Szlyk (1985). Ventilation and respiratory pattern and timing in resting awake cats. *Can. J. Physiol. Pharmacol.* 63: 148–154.

Kay, J.D.S., E. Strange Petersen and H. Vejby-Christensen (1975a). Breathing in man during steady-state exercise on the bicycle at two pedalling frequencies, and during treadmill walking. *J. Physiol.* 251: 645–656.

Kay, J.D.S., E. Strange Petersen and H. Vejby-Christensen (1975b). Mean and breath-by-breath pattern of breathing in man during steady-state exercise. *J. Physiol.* 251: 657–669.

Kelman, G.R. and A.W.S. Watson (1973). Effect of added dead-space on pulmonary ventilation during submaximal, steady-state exercise. *Quart. J. Exp. Physiol.* 58: 305–313.

McMurray, R.G. and S.W. Ahlborn (1982). Respiratory responses to running and walking at the same metabolic rate. *Respir. Physiol.* 47: 251–265.

Milic-Emili, G. and M.M. Grunstein (1976). Drive and timing components of ventilation. *Chest* 70, Suppl.: 131–133.

Newsom-Davis, J. and D. Stagg (1975). Interrelationships of the volume and time components of individual breaths in resting man. *J. Physiol. (London)* 245: 481–498.

Sipple, J.H. and R. Gilbert (1966). Influence of proprioceptor activity in the ventilatory response to exercise. *J. Appl. Physiol.* 21: 143–146.

Sullivan, C.E., L.F. Kozar, E. Murphy and E.A. Phillipson (1978). Primary role of respiratory afferents in sustaining breathing rhythm. *J. Appl. Physiol.: Respir. Environ. Exercise Physiol.* 45: 11–17.

Szlyk, P.C. and D.B. Jennings (1987). Effects of hypercapnia on variability of normal respiratory behavior in awake cats. *Am. J. Physiol.* 252: R538–R547.